Insects Associated with Scolytidae (Coleoptera) in Western Washington

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The importance of scolytids as enemies of forest trees has inspired a number of studies of the insects, including predators and parasitoids, associated with scolytids. Several large-scale studies deal with the associates of a single species of scolytid (DeLeon, 1934; Bedard, 1938; Ashraf and Berryman, 1969; Dahlsten, 1970; Moser *et al.*, 1971). A few additional studies deal with all the scolytid associates occurring in one tree species (Pechuman, 1937; Reid, 1957, 1957a; Deyrup, 1975, 1976). There are a few compendia of associates of Nearctic scolytids (Chamberlin, 1939; Bushing, 1965; Bushing and Bright, 1965). The present study differs from the works cited above in that it is an attempt to survey the associates of all common scolytids in all their host trees within a relatively small geographic area.

Materials and Methods

Scolytids and their associates were sampled in 2 intensive study sites and 35 minor study sites, all in western Washington. The intensive sites are 1) a stable predominantly Douglas-fir and hemlock second-growth stand of trees that are mostly 30 to 60 cm. dbh., in the Cedar River watershed, near Cedar Falls, King Co., Wash., elev. 290 m.; 2) an area of poorly growing overstocked second- and third-growth Douglas-fir and lodgepole pine at Bear Lake, 11 km. S. of Bremerton, Kitsap Co., Wash., elev. 135 m.

All species listed were obtained by opening scolytid galleries and removing the associates along with a sample of the hosts. All Diptera, Hymenoptera, Hemiptera, and many of the Coleoptera were taken as larvae or pupae and reared to maturity. The live insects, often accompanied by bits of wood or bark, were placed on a small pad of paper toweling in 100 x 15 mm Optilux Petri dishes (Falcon Plastics, Oxnard, Calif.). The paper toweling was moistened with a few drops of water every other day. Predacious and scavenging insects were fed living or dead larvae of scolytids. The great majority of insects reared were brought indoors in late winter or spring after diapause had been naturally broken.

Determinations were made by Dr. Bernard Burks (Eupelmidae), Dr. Raymond Gagne (Cecidomyiidae), Dr. Paul Marsh (Braconidae), Dr. Curtis Sabrosky (Chloropidae), and Mr. George Steyskal (Odiniidae, Pallopteridae), at the U.S. National Museum; Dr. Robert Bugbee

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(Eurytomidae) at Allegheny College, Meadville, Penn.; Dr. Fred Harmston (Dolichopodidae) of the U.S. Public Health Service, Ft. Collins, Col.; and Dr. M. Deyrup (remaining families of associates), University of Washington, Seattle.

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Factors Influencing Scolytid Associates

The results of this study show that within a limited geographic area scolytid associates tend to occur in galleries of several species of scolytids and in two or more species of tree hosts. Thus, the local populations of enemies of one species of scolytid may be largely regulated by the abundance of alternate hosts, a factor not always considered in studies of population dynamics of scolytids and their enemies. The present study, as well as the published lists (cited above) of associates of individual species of scolytids, indicates that each species of scolytid may support many species of associates. The associates of scolytids must be directly influenced by factors other than host species, and occupy a diversity of trophic roles.

One factor of great importance to all insects inhabiting dead trees is the amount of exposure of the tree to direct sunlight. The importance of exposure is undoubtedly mostly environmental: an insect in exposed bark must be physiologically adapted to high temperatures, rapid temperature fluctuations, and accelerated dessication, while an insect in shaded bark must be adapted to cooler, more even temperatures, and to greater moisture (Graham, 1925). Not only environmental conditions are determined by exposure to sunlight, but also the mechanisms by which hosts are located. The host tree is probably initially located by odor, and chemical compounds emanating from exposed trees seem to differ from those emanating from shaded trees (Stoszek, 1973). Parasitoids that pinpoint their hosts by the minute amount of heat generated by each subcortical larva (Richerson and Borden, 1972) are probably unable to find hosts on sunlit bark because of the variability of heat absorption and reflection on the irregular surface. During the present study it was found that the wasps *Cecidostiba acuta* (Provancher), *Heydenia unica* Cook and Davis, *Spathius sequoiae* Ashmead, *Ecphylus pacificus* Marsh, and *Eurytoma tomici* Ashmead usually oviposit on hosts in shaded bark; *Cecidostiba thomsoni* Crawford, *Cheiropachus brunneri* Crawford, *Ecphylus californicus* Rhower, and *Eurytoma phloeotribi* Ashmead usually oviposit on hosts in exposed bark.

Another ecological factor that is of obvious importance to most parasitoids of scolytids is the thickness of the bark separating the parasitoid from its subcortical host. Except for those few species

that attack adult scolytids (*Karpinskiella, Tomicobia*) or enter the scolytid egg gallery (*Roptrocerus, Ipideurytoma*), parasitoids of scolytids are limited by the length of their ovipositors. In some cases (e.g. *Spathius* vs. *Ecphylus*) this provides a possible niche separation of the sort made famous by Heatwole and Davis (1965) in their study of *Megarhyssa* species. The importance of bark thickness is greatly accentuated by two factors: parasitoids of scolytids are necessarily small because of the smallness of their hosts, and the ovipositor, for unknown reasons, is almost never much longer than the combined length of the head and body. An unusually large specimen (actually reared from a large subcortical weevil) of the largest parasitoid of scolytids in western Washington has an ovipositor about 8 mm. long, and the principle host of this species is a scolytid often found under bark several centimeters thick.

Predators, which always enter scolytid gallaries through holes made by the scolytids themselves, are not strongly influenced by bark thickness, but are strongly influenced by prey density as it is difficult to force passage through intact inner bark. This is particularly true of larvae of flies, such as *Medetera* (Nagel and Fitzgerald, 1975) but also applies to beetles. As might be expected, these predators show opportunistic behavior. Some predators, such as *Thanasimus undatulus* Say, *Temnochila chlorodia* (Mannerheim), *Xylophagus abdominalis* Loew, *Ampedus anthracinus* LeConte, and *Lasconotus intricatus* Kraus feed, at least in the laboratory, on any available insect larvae or pupae, including those of parasitoids and other predators. Species of scolytids that attack trees in early spring, producing a single brood that abandons the tree in summer (e.g. *Pseudohylesinus nebulosus* (LeConte)) are able to convert natural enemies into assets as the predators do most of their feeding when there are only parasitoids, predators, and inquilines remaining in the tree. Other predators, such as some species of *Lonchaea, Corticeus,* possibly *Palloptera,* seem to be primarily scavengers and only facultative predators. A number of predators, or supposed predators, such as *Lasconotus, Lonchaea,* possibly *Gaurax,* minimize host searching by their ability to develop to maturity, at least in the laboratory, on a single host larva or pupa.

For scolytid parasitoids, which are compelled to complete development on a single host, the size of the host larva is an important and complicated factor. Successful parasitism of hosts that are much larger than normal is rare; possibly there is heavy mortality of parasitoid pupae when the pupal cell is occupied by the decomposing remains of an unconsumed host larva, or perhaps large hosts tend to recover rapidly and crush the egg of the parasitoid. Successful parasitism of hosts that are smaller than normal is commonplace and seems to present the parasitoid with both liabilities and benefits. The principle liability is that subnormal hosts produce miniature adult

parasitoids. Small males may be at a disadvantage when competing for mates. Small females have a graver disability as the length of the ovipositor remains proportional to body size so that the number of hosts available to small females may be seriously reduced. The females also need stored energy supplies for flying to a new host tree (males remain on the natal tree) and for egg production. Thus, the wasp that oviposits on undersized hosts seems to be spending much time and effort producing poorly adapted offspring. On the other hand, parasitization of undersized host larvae is highly advantageous when the only hosts available are small, either because it is early in the season and the hosts are young, or because only small species of bark beetles have infested the tree. In these situations a generation of small parasitoids may be produced that will bridge the gap of time or space separating the parent parasitoid from ideal hosts. When there are both large and small hosts in a tree the ovipositing parasitoid may be able to lay male (unfertilized) eggs on small hosts and female (fertile) eggs on larger hosts, a discrimination of great value since small males are less at a disadvantage than small females. This mechanism, first noted by Ryan (1961) in the scolytid parasitoid *Coeloides brunneri* Viereck, has been observed during the present study in *Spathius, Ecphylus,* and *Cecidostiba.*

The influence of tree host species on scolytid associates is not well understood. Eastern species of *Spathius* seem to be clearly divided into a group of conifer inhabitants and a group associated with broadleaf trees (Matthews, 1970), but during the present study in western Washington *S. sequoiae* Ashmead was found in alder as well as in numerous species of conifers. Berisford and Franklin (1972) have shown that of four species of pine attacked by *Ips* two species are preferred by the parasitoid *Heydenia unica* Cook and Davis regardless of the number or species of the bark beetle hosts in the trees. It is perhaps significant that the two preferred pines are indigenous to the study area while the other two pines are introduced. The influence of the tree host on associates of scolytids will probably remain obscure until there is more information on how the associates find scolytid-infested trees.

It is logical to expect that some associates of scolytids are attracted by host pheromones; such associates should show considerable host-specificity. Associates that occur in well-developed scolytid galleries arrive long after pheromone production has presumably ceased, but predators and parasitoids that attack adult scolytids which are boring into host trees should be able to use pheromones to find their temporarily exposed hosts. Attraction to host pheromones has been shown in the parasitoid *Tomicobia tibialis* Ashmead (Rice, 1968), and in the predators *Enoclerus lecontei* Wolcott (Rice, 1969), *Thanasimus undatulus* Say (Pitman and Vite, 1970; Kline *et al.*, 1974), and *Temnochila chlorodia* Mannerheim (Bedard *et al.*, 1969; Pitman and Vita, 1971). None of these species, however, shows a high

degree of host specificity. *Tomicobia tibialis* attacks at least 6 species of *Ips* (Bushing, 1965); a European species *T. seitneri* (Ruschka) also attacks several species of *Ips,* though a third species, *T. accuminati* Hedqvist attacks only *Ips accuminatus* (Gyllenhal) (Hedqvist, 1963). The genus *Karpinskiella,* also parasitoids of adult scolytids, has not been studied extensively, but seems to be more host specific than *Tomicobia* (Hedqvist, 1963; Furniss, 1968). Parasitoids of adult scolytids may be confined to a single genus of hosts, but the predators lack even this degree of host specificity and often occur on trees infested with scolytids other than those whose pheromones are known to attract the predators. These predators must either respond to a remarkable range of host pheromones (or tree odors) or else are divided into populations having differing responses to pheromones of locally abundant scolytids.

The presence of some scolytid associates is clearly determined by the fungal flora of the scolytid galleries. Species that feed directly on fungus include *Renardia nigrella* Motschulsky, *Scatopsciara* sp., and *Asynapta* sp. These are attended by a group of predators that includes *Isolomalus mancus* Casey, *Nudobius cephalus* Say, and *Medetera arctica* VanDuzee. Many other associates whose diet is unknown may also feed on fungi.

List of Records

A list of scolytids and their associates follows. An asterisk indicates an association not previously reported in the literature.

Alniphagus aspericollis (LeConte)
- **Acrulia tumidula* Maklin
- **Atheta* sp.
- **Calosota pseudotsugae* Burks
- **Cecidostiba acuta* (Provancher)
- **Renardia nigrella* Motschulsky
- **Rhinosiums viridiaeneus* Randall
- **Spathius sequoiae* Ashmead

Carphoborus vandykei Bruck
- **Ampedus anthracinus* LeConte
- **Calosota pseudotsugae* Burks
- **Ecphylus californicus* Rohwer
- **Eupelmella vesicularis* (Retzius)
- **Eurytoma phloeotribi* Ashmead
- **Gaurax dubius* (Macquart)
- **Heydenia unica* Cook and Davis
- **Lasconotus intricatus* Kraus
- **Macromesus americanus* Hedqvist
- **Nemosoma attenuatum* Van Dyke
- **Roptrocerus xylophagorum* Ratzeburg
- **Scoloposcelis flavicornis* Reuter
- **Spathius sequoiae* Ashmead

Cryphalus pubescens (Hopkins)
- **Asynapta* sp.
- **Calosota pseudotsugae* Burks
- **Cecidostiba acuta* (Provancher)
- **Ecphylus pacificus* Marsh
- **Karpinskiella* sp. A
- **Spathius sequoiae* Ashmead

Dendroctonus pseudotsugae Hopkins
- *Atheta* sp.
- *Atrechus macrocephalus* Nordmann
- *Coeloides brunneri* Viereck
- **Corticeus strublei* Blaisdell
- *Cucujus clavipes* Fabricius
- *Enoclerus sphegeus* Fabricius
- *Isolomalus mancus* Casey
- **Leptothorax acervorum* Fabricius
- **Leptusa* sp.
- *Lonchaea furnissi* McAlpine
- *Medetera aldrichii* Wheeler
- **M. arctica* VanDuzee
- **M. vidua* Wheeler
- *Nudobius cephalus* Say

Phloeonomus pusillus Gravenhorst
**Placusa* sp.
Psilis atricornis (Ashmead)
Quedius laevigatus Gyllenhal
Renardia nigrella Motschulsky
Rhizophagus dimidiatus Mannerheim
**R. grouvellei* Mequignon
Spathius sequoiae Ashmead
Temnochila chlorodia (Mannerheim)
Thanasimus undatulus Say
Xylophagus abdominalis Loew

Dryocoetes autographus Ratzeburg
**Medetera aldrichii* Wheeler
**Medetera* sp. A

Gnathotrichus retusus (LeConte)
**Chymomyza aldrichii* Sturtevant

Gnathotrichus sulcatus (LeConte)
**Chymomyza aldrichii* Sturtevant

Hylurgops rugipennis (Mannerheim)
**Cecidostiba acuta* (Provancher)
Medetera aldrichii Wheeler

Ips concinnus (Mannerheim)
Medetera sp. B
**Xylophagus abdominalis* Loew

Ips mexicanus (Hopkins)
**Agathidium obtusum* Hatch
**Nudobius cephalus* Say
**Platysoma punctigerum* LeConte
**Renardia nigrella* Motschulsky
**Zabrachia polita* Coquillett

Ips perturbatus (Eichhoff)
**Atrechus macrocephalus* Nordmann
**Dolurgus pumilus* (Mannerheim)
**Medetera aldrichii* Wheeler
**M. arctica* VanDuzee
**M. vidua* Wheeler
**Quedius laevigatus* Gyllenhal
**Xylophagus abdominalis* Loew

Orthotomicus caelatus (Eichhoff)
Cucujus clavipes Fabricius
**Eupelmella vesicularis* (Retzius)
**Gaurax dubius* (Macquart)
Isolomalus mancus Casey
Lasconotus subcostulatus Kraus
**Leptothorax acervorum* Fabricius
**Lonchaea corticis* Taylor
**Medetera arctica* Van Duzee
Medetera sp. A
**Megaselia* sp.
Nudobius cephalus Say
**Phloeopora oregona* Casey
Platysoma punctigerum LeConte
**Scatopsciara* sp.
**Scoloposcelis flavicornis* Reuter
**Spathius sequoiae* Ashmead
**Xylocoris* sp.
Xylophagus abdominalis Loew

Phloeosinus punctatus LeConte
**Cecidostiba acuta*'(Provancher)
**Gaurax dubius* (Macquart)
**Lasconotus intricatus* Kraus
**Palloptera terminalis* Loew
**Phloeonomus pusillus* Gravenhorst
Spathius sequoiae Ashmead

Phloeotribus lecontei LeConte
Karpinskiella sp. B

Pityophthorus confertus Swaine
**Gaurax dubius* (Macquart)
**Lasconotus intricatus* Kraus
**L. pertenuis* Casey
**L. planipennis* Kraus
**Medetera arctica* VanDuzee
**Palloptera terminalis* Loew
**Renardia nigrella* Motschulsky
**Rhizophagus minutus* Mannerheim
**Roptrocerus xylophagorum* Ratzeburg
**Scoloposcelis flavicornis* Reuter
**Xylocoris* sp.

Pityophthorus nitidulus (Mannerheim)
**Cecidostiba acuta* (Provancher)

Pityophthorus pseudotsugae Swaine
**Corticeus occidentalis* Wallis
**Lonchaea corticis* Taylor
**Palloptera terminalis* Loew
**Phloeonomus pusillus* Gravenhorst
**Phloeopora oregona* Casey
**Rhizophagus minutus* Mannerheim
**Roptrocerus xylophagorum* Ratzeburg

Pseudohylesinus granulatus LeConte
**Acrulia tumidula* Maklin
**Medetera aldrichii* Wheeler

Pseudohylesinus nebulosus (LeConte)
**Acrulia tumidula* Maklin
**Atheta* sp.
**Atrechus macrocephalus* Nordmann
**Blacus* sp.
**Calosota pseudotsugae* Burks
Cecidostiba acuta (Provancher)
Cheiropachus brunneri Crawford

Coeloides brunneri Viereck
**Corticeus strublei* Blaisdell
**Dolurgus pumilus* (Mannerheim)
**Eurytoma tomici* Ashmead
**Gaurax dubius* (Macquart)
Heydenia unica Cook and Davis
**Lasconotus intricatus* Kraus
**Leptusa* sp.
Macromesus americanus Hedqvist
**Medetera arctica* VanDuzee
**Nemosoma attenuatum* Van Dyke
**Phloeopora oregona* Casey
**Placusa* sp.
**Renardia nigrella* Motschulsky
**Rhizophagus dimidiatus* Mannerheim
Roptrocerus xylophagorum Ratzeburg
**Spathius aphenges* Matthews
S. sequoiae Ashmead
**Thanasimus undatulus* Say

Pseudohylesinus sericeus (Mannerheim)
**Acrulia tumidula* Maklin
**Atheta* sp.
Cecidostiba acuta (Provancher)
Coeloides brunneri Viereck
**Eurytoma tomici* Ashmead
Medetera aldrichii Wheeler
**Phloeopora oregona* Casey
**Rhizophagus dimidiatus* Mannerheim
Roptrocerus xylophagorum Ratzeburg
Spathius sequoiae Ashmead
**Thanasimus undatulus* Say

Pseudohylesinus sitchensis Swaine
**Cecidostiba acuta* (Provancher)

Pseudohylesinus tsugae Swaine
**Cecidostiba acuta* (Provancher)

Scolytus rugulosus Ratzeburg
Cheiropachus quadrum (Linneus)

Scolytus unispinosus LeConte
**Agathidium obtusum* Hatch
**Asynapta* sp.
**Cecidostiba thomsoni* Crawgord
Cheiropachus brunneri Crawford
**Coeloides brunneri* Viereck
**Corticeus strublei* Blaisdell
**Ecphylus californicus* Rohwer
**Enoclerus barri* Knull
E. lecontei Wolcott
**Eurytoma phloeotribi* Ashmead
**E. tomici* Ashmead
**Gaurax dubius* (Macquart)
**Heydenia unica* Cook and Davis
**Lasconotus subcostulatus* Kraus
**L. pertenuis* Casey
**Lonchaea corticis* Taylor
Macromesus americanus Hedqvist
**Medetera arctica* VanDuzee
**Palloptera terminalis* Loew
**Phloeonomus pusillus* Gravenhorst
**Renardia nigrella* Motschulsky
**Rhizophagus dimidiatus* Mannerheim
**R. grouvellei* Mequignon
**R. minutus* Mannerheim
**Spathius sequoiae* Ashmead
Spathius undatulus Say

Trypodendron lineatum (Olivier)
**Chymomyza aldrichii* Sturtevant
**Epuraea* sp.
**Odinia betulae* Sabrosky

Annotated List of Insects Associated with Scolytids in Western Washington

Acrulia tumidula Maklin (Staphylinidae)
Adults occur in galleries of scolytids in shaded conifers and broadleaf trees, sometimes in rotten wood or under bark of trees not infested with scolytids; diet unknown.

Agathidium obtusum Hatch (Leiodidae)
Adults occur in recently abandoned galleries of scolytids in shaded and exposed conifers; probably scavengers.

Ampedus anthracinus LeConte (Elateridae)
Larvae are predators in galleries of subcortical insects in shaded or partially exposed conifers.

Asynapta sp. (Cecidomyiidae)
Larvae feed on fungi in egg galleries of small scolytids in conifers and alder.

Atheta sp. (Staphylinidae)
Adults occur in galleries of scolytids, subcortical weevils and cerambycids in shaded conifers; diet unknown.

Atrechus macrocephalus Nordmann (Staphylinidae)
Adults and larvae occur in abandoned galleries of scolytids in shaded conifers; diet is probably fly larvae.

Blacus sp. (Braconidae)
Adults of this undescribed species enter galleries of *Pseudohylesinus nebulosus* to parasitize larval *Lasconotus intricatus.*

Calosota pseudotsugae Burks (Eupelmidae)
Larvae are hyperparasitoids within the cocoons of *Spathius sequoiae* in galleries of small scolytids in shaded conifers and alder.

Cecidostiba acuta (Provancher) (Pteromalidae)
Larvae are parasitoids of small scolytid larvae in shaded conifers and alder.

Cecidostiba thomsoni Crawford (Pteromalidae)

Cheiropachus brunneri Crawford (Pteromalidae)
Larvae of both species are parasitoids of small scolytid larvae in exposed conifers.

Cheiropachus quadrum (Linneus) (Pteromalidae)
Larvae are parasitoids of *Scolytus rugulosus* larvae in *Prunus.*

Chymomyza aldrichii Sturtevant (Drosophilidae)
Larvae occur in galleries of ambrosia beetles in conifers and probably feed on fungi.

Coeloides brunneri Viereck (Braconidae)
Larvae are parasitoids of large scolytid and subcortical weevil larvae in shaded conifers.

Corticeus occidentalis Wallis (Tenebrionidae)
Adults and larvae occur in galleries of *Pityophthorus pseudotsugae* in *Abies;* probably fungus feeders and facultative predators.

Corticeus strublei Blaisdell (Tenebrionidae)
Adults and larvae occur in scolytid galleries, usually in shaded conifers; probably fungus feeders and facultative predators.

Cucujus clavipes Fabricius (Cucujidae)
Larvae are predators in galleries of cerambycids and large scolytids in shaded conifers.

Dolurgus pumilus (Mannerheim) (Scolytidae)
Adults and larvae are inquilines feeding on bark within the galleries of larger scolytids.

Ecphylus bicolor Rohwer (Braconidae)
Larvae are parasitoids of *Pityophthorus* larvae in pine.

Ecphylus californicus Rohwer (Braconidae)
Larvae are parasitoids of small scolytid larvae in exposed or semi-

exposed conifers.

Ecphylus pacificus Marsh (Braconidae)

Larvae are parasitoids of *Cryphalus pubescens* larvae in shaded Douglas-fir twigs.

Enoclerus barri Knull (Cleridae)

Larvae and adults are predators of small scolytids in exposed conifers.

Enoclerus lecontei Wolcott (Cleridae)

Larvae and adults are predators of small and medium-sized scolytids in exposed or semiexposed conifers.

Epuraea truncatella Mannerheim (Nitidulidae)

Adults occur in galleries of *Dendroctonus pseudotsugae* and *Pissodes fasciatus* in shaded Douglas-fir; diet unknown.

Epuraea sp. (Nitidulidae)

Adults occur in galleries of *Trypodendron lineatum;* diet unknown.

Eupelmella vesicularis (Retzius) (Eupelmidae)

Larvae are parasitoids of a great variety of hosts (Deyrup, 1975), occasionally occuring as a hyperparasitoid of chalcidoids in galleries of small scolytids.

Eurytoma phloeotribi Ashmead (Eurytomidae)

Larvae are parasitoids of small scolytid larvae in exposed or semi-exposed conifers.

Eurytoma tomici Ashmead (Eurytomidae)

Larvae are parasitoids of small scolytid larvae, usually in shaded conifers.

Gaurax dubius (Macquart) (Chloropidae)

Larvae occur in galleries of small scolytids in conifers; probably scavengers.

Heydenia unica Cook and Davis (Pteromalidae)

Larvae are parasitoids of small scolytid larvae, usually in shaded conifers.

Isolomalus mancus Casey (Histeridae)

Adults and larvae occur in galleries of large scolytids in conifers, sometimes a year or more after the departure of the scolytids; probably predators feeding on fly larvae.

Karpinskiella sp. A (Pteromalidae)

Larvae are internal parasitoids of adult *Cryphalus pubescens* in Douglas-fir; this species is apparently undescribed.

Karpinskiella sp. B (Pteromalidae)

Larvae are internal parasitoids of adult *Phloeotribus lecontei* in *Abies;* another undescribed species.

Lasconotus intricatus Kraus (Colydiidae)

Adults and larvae occur in galleries of small scolytids in shaded conifers; larvae are predators of scolytid larvae and their parasitoids.

Lasconotus pertenuis Casey (Colydiidae)

Lasconotus planipennis Kraus (Colydiidae)

Adults and larvae of both species occur rarely in galleries of small scolytids in pine; probably predators.

Lasconotus subcostulatus Kraus (Colydiidae)

Adults and larvae are predators and fungus-feeders in galleries of small scolytids in exposed conifers.

Leptothorax acervorum Fabricius (Formicidae)

Colonies occur in abandoned galleries of cerambycids, buprestids, and scolytids in conifers and broadleaf tree; colonies occasionally in unabandoned galleries of *Dendroctonus;* a colony in the laboratory consumed cerambycid larvae but rejected scolytid larvae.

Leptusa sp. (Staphylinidae)

Adults occur in galleries, often abandoned galleries, of scolytids, curculionids, and cephaloids in shaded conifers; diet unknown.

Lonchaea corticis Taylor (Lonchaeidae)

Larvae are scavengers or facultative predators of scolytids and weevils in exposed conifers.

Lonchaea furnissi McAlpine (Lonchaeidae)

Larvae are scavengers in galleries of *Dendroctonus* and *Pissodes* in shaded Douglas-fir.

Macromesus americanus Hedqvist (Pteromalidae)

Larvae are parasitoids of small scolytid larvae, usually in exposed conifers.

Medetera aldrichii Wheeler (Dolichopodidae)

Larvae are predators in galleries of scolytids in shaded conifers.

Medetera arctica VanDuzee (Dolichopodidae)

Larvae are predators in galleries of scolytids in conifers, often occur under bark where only other fly larvae are present.

Medetera vidua Wheeler (Dolichopodidae)

Larvae are predators in galleries of scolytids and curculionids in shaded conifers; this species prefers a moister habitat than that preferred by *M. aldrichii* and *M. arctica.*

Medetera sp. A (Dolichopodidae)

Larvae of this unidentified bluish species are predators in galleries of scolytids in Douglas-fir and pine.

Medetera sp. B (Dolichopodidae)

Larvae of this large apparently undescribed species with a dark area around the medial cross-vein were reared from galleries of *Ips* in spruce.

Nemosoma attenuatum Van Dyke (Trogositidae)

Adults and larvae occur in galleries of small scolytids in conifers; probably predators.

Nudobius cephalus Say (Staphylinidae)

Adults and larvae occur in galleries of scolytids in semiexposed conifers; probably predators on larval insects in scolytid egg galleries.

Odinia betulae Sabrosky (Odiniidae)

Larvae occur in galleries of *Trydodendron* in conifers and broadleaf trees; probably predators.

Palloptera terminalis Loew (Pallopteridae)

Larvae feed on dead scolytid larvae in exposed conifers.

Phloeonomus pusillus Gravenhorst (Staphylinidae)

Phloeopora oregona Casey (Staphylinidae)

Adults of both species occur in galleries of scolytids in conifers; diet unknown.

Placusa sp. (Staphylinidae)

Adults occur in galleries of *Pseudohylesinus* and *Dendroctonus* in shaded conifers; diet unknown; probably an undescribed species.

Platysoma punctigerum LeConte (Histeridae)

Adults and larvae are predators in galleries of scolytids in pine.

Psilus atricornis (Ashmead) (Diapriidae)

Larvae are parasitoids of *Lonchaea corticis* pupae in galleries of large scolytids in conifers; this species does not attack *L. corticis* in leaders of *Picea.*

Quedius laevigatus Gyllenhal (Staphylinidae)

Adults and larvae are predators in occupied or abandoned galleries of large scolytids in shaded conifers.

Renardia nigrella Motschulsky (Staphylinidae)

Adults and larvae feed on fungi in galleries of scolytids in conifers and alder.

Rhinosimus viridiaeneus Randall (Salpingidae)

Larvae and probably adults as well, feed on fungus in galleries of *Alniphagus* in alder; also occur under bark of broadleaf trees not inhabited by scolytids.

Rhizophagus dimidiatus Mannerheim (Rhizophagidae)

Rhizophagus grouvellei Mequignon (Rhizopagidae)

Adults and larvae of both species occur in galleries of scolytids in conifers; probably predators.

Rhizophagus minutus Mannerheim (Rhizophagidae)

Adults and larvae occur in galleries of small scolytids in exposed conifers; probably a predator.

Roptrocerus xylophagorum Ratzeburg (Torymidae)

Larvae are parasitoids of small scolytid larvae in conifers.

Scatopsciara sp. (Sciaridae)

Larvae are scavengers or fungus feeders in galleries of scolytids.

Scoloposcelis flavicornis Reuter (Anthocoridae)

Adults and nymphs are predators in galleries of scolytids in exposed or semiexposed conifers.

Spathius sequoiae Ashmead (Braconidae)

Larvae are parasitoids of small scolytid larvae in shaded or semi-exposed conifers.

Temnochila chlorodia (Mannerheim) (Trogositidae)

Adults and larvae are predators of large scolytids in semiexposed conifers.

Thanasimus undatulus Say (Cleridae)

Adults and larvae are usually predators of *Pseudohylesinus* species in shaded conifers.

Xylocoris sp. (Anthocoridae)

Adults and nymphs are predators in galleries of scolytids and cerambycids in exposed conifers.

Xylophagus abdominalis Loew (Xylophagidae)

Larvae are general predators under bark of conifers.

Zabrachia polita Coquillett (Stratiomyidae)

Larvae occur in galleries of scolytids in conifers; probably a scavenger.

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